South African Journal of Botany 2005, 71(1): 53–60

SOUTH AFRICAN JOURNAL OF BOTANY
EISSN 1727–9321

The effect of fire on the soil seed bank of a semi-arid grassland in South Africa

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Received 17 November 2003, accepted in revised form 23 June 2004

During the dormant winter period the semi-arid grassland areas of South Africa are characterised by planned and unplanned fires, either by lightning or negligence by man. The influence of burning (head and back fire) on the germinability of grass species in the soil seed bank was quantified in the greenhouse over the 2000/01 to 2001/02 growing seasons for a semi-arid grassland. The behaviour of the head and back fires was also monitored. Soil seed bank samples were collected immediately after burning and then every third month over a two-year period from 0.25m² blocks 50mm deep. The same was done on unburnt grassland. At ground level, the back fire exceeded 100°C, while the head fire had temperatures of less than 100°C. The fire caused a flush of seedlings from the seed bank over the first season after the fire. The head fire stimulated seedling density significantly (P ≤ 0.01) more than the back fire. The mean (head and back fire) seed bank density the first season following the fire, for burnt and unburnt grassland, was respectively 84.6 and 52.1 grass seedlings m⁻² for September, 50.5 and 21.9 grass seedlings m⁻² for December and 347 and 58 grass seedlings m⁻² for March. The pioneer species *Aristida congesta* and *Tragus koelerioides* only occurred in the soil seed bank of the burnt grassland, while the climax species *Cymbopogon plurinodes*, *Digitaria eriantha* and *Panicum stapfianum* only germinated in the unburnt grassland seed bank. The *Eragrostis* species showed the highest germination due to fire. The burning of semi-arid grassland did have a quantified impact on the soil seed bank over the short-term.

Introduction

Fire is a natural phenomenon in semi-arid grassland areas of southern Africa (Everson 1999) and may have a negative effect on grassland functioning by the reduction or elimination of above-ground biomass (Snyman 2003a, 2004a), the reduction of below-ground physical, chemical and microbial- mediated processes (Neary *et al*. 1999, Snyman 1999, 2003b), or altering the size and composition of the soil seed bank (Skoglund 1992). The common practice of communal livestock farmers in these areas, of grazing grassland following burning when grass species are in full flower (Everson 1999), exacerbates degradation by depressing seed production. It is important to understand the ecology of these grasslands if productivity is to be increased and erosion reduced.

Relatively little recent research work on grassland burning has been done in the drier grassland regions of southern Africa and it has generally been assumed that fire should be excluded from these types of grassland (Everson 1999, Snyman 2002, 2003a, 2004a). For example, yield measurements and seedling emergence have seldom been noted in grassland burning experiments and most assessments of the effects of burning have been based on visual ratings. Therefore, these unplanned events can have a major influence on the short-term functioning of the ecosystem, especially in drier areas (Snyman 1998, Oesterheld *et al*. 2001).

Soil seed banks are important components of vegetation dynamics affecting both ecosystem resistance and resilience (Pugnaire and Lazaro 2000). A phenomenon common to many grassland communities is the flush of germination that follows a burn (Specht *et al*. 1958, Le Houérou 1973, Whelan 1988, Tyler 1995). In recent years there has been an escalating interest in seed banks of grassland ecosystems. Factors affecting germination and early seedling growth are often the primary determinants of the distribution of adult plants (De Jong and Klinkhamer 1988, Mustart and Cowling 1993). Therefore, to understand the dynamics of communities, specifically in drier areas, knowledge of seedling responses to different environmental conditions is often of prime importance (De Villiers *et al*. 2001, Kinloch and Friedel 2005a, 2005b).

The burning of semi-arid grassland has an important impact on the seasonal establishment and survival of seedlings over the short-term and therefore the functioning of the grassland ecosystem (Snyman 2004b). In this study the influence of a head vs a back fire on the soil seed bank of a grassland in a semi-arid climate is explored. The recruitment of grass species from the soil seed bank, after different fire treatments over two growing seasons in the greenhouse, is reported.

Material and Methods

Site description and treatments

The study was conducted at Bloemfontein (28°50'S, 26°15'E, altitude 1 350m), situated in the semi-arid, summer rainfall region (mean annual rainfall 560mm) of South Africa. Rain falls almost exclusively during summer (October to April), with a mean of 78 rainy days per year. Mean maximum monthly temperatures range from 17°C in July to 33°C in January, with a mean of 119 frost days per annum (ISCW Data Bank 1998).

Grassland in good ecological condition, typical of the dry Sandy Highveld Grassland in the Grassland Biome (Bredenkamp and Van Rooyen 1996) was selected for this study. The botanical composition and basal cover of the grassland in good condition was typical of that on commercial farms in the area. The soil is a fine sandy loam Rhodic Epigleyic Luvisol (FAO 1998). Clay content increases with soil depth from 10% in the A-horizon (0–300mm), to 24% in the B1-horizon (300–600mm) and 42% in the B2-horizon (600–1 200mm).

The research was conducted on 18 plots of 10m x 10m each, with a buffer zone of 5m around every plot. This was a one-off burn. The three treatments included fire burning against the wind (back fire), with the wind (head fire) (Trollope 1978), and a control with no burning over the last 15 years. The treatments were randomly allocated to the plots. Six plots were burnt on 30 August 2000 and another six on 23 August 2001. The burnt plots were therefore burnt only once during the two-year trial period. The head and back fire treatments were applied on the same day to ensure that the two types of fires were comparable. The burn treatments were applied each year at the end of August after spring rainfall thoroughly wetted the soil, causing the grass sward to become relatively green. Burning was carried out in the morning with a light wind blowing. To limit the fire to every burnt plot, the plants surrounding each plot were cut short and soaked before burning. The plots were excluded from any grazing over the two-year trial period.

Data collection

The estimation of fuel load and fuel-water content before the burning was fully discussed by Snyman (2004b). The mean length of the flames was estimated visually once the fire was burning uniformly. The rates at which the head and back fires moved over the plots were measured by a stopwatch. The wind velocity was recorded at the start, during and at the end of the fire with a hand-held anemometer at a height of approximately 1.7m. Air temperature and relative humidity were measured immediately prior to burning with a whirling psychrometer.

The fire behaviour model of Trollope (1999) was used to predict the fire intensities to which the treatment blocks were subjected for each season's burning (Snyman 2004b). Fire intensities were estimated and classified into one of the categories proposed by Trollope and Potgieter (1985). The procedure for recording fire intensity (10mm under the soil, at ground level, grass canopy height and 1m above ground level) by chrome-alumel thermocouples connected to a portable electronic temperature recorder was fully discussed by Snyman (2003a). The mean grass canopy height was 230 ± 25mm for the August 2000 and August 2001 fires. Botanical composition before burning was determined with a bridge-point apparatus (Walker 1970, Snyman and Fouché 1991), where 500 points (nearest plant) were recorded per plot before the fire as well as four months after the fire. Grassland condition was assessed according to the method of Fourie and Du Toit (1983). Species were classified in terms of grazing value (dry-matter production, palatability, nutritive value, whether perennial or annual and grazing resistance) and the ecological status (decreaser and increaser species) as defined by Foran *et al*. (1978). The classifications of dry *Themeda–Cymbopogon* grassland into different ecological groups, as described by Fourie and Visagie (1985), was used.

Within each treated plot, eight randomly-distributed soil samples of 0.5m x 0.5m each were collected to a depth of 50mm. Only the soil between the tufts was sampled. Samples were collected into separate paper bags for immediate transport to the greenhouse for processing within 10min of collection. In the greenhouse, soil samples were spread evenly in plastic containers (0.5m x 0.5m) containing a 100mm deep layer of Hygiotech growth medium (Canadian peat, polystyrene vermiculite and mono-ammonium phosphate). To measure the extent of contamination, eight additional plastic containers filled with autoclave-sterilised soil (90°C for 1h — repeated three times over a week) were included with each set of soil samples. Seedling plastic containers were placed at random in the greenhouse. Containers were hand-watered daily, after which the seedlings were identified and counted daily over a two-month period. All identifiable seedlings were removed. Seedlings that could not be identified after two months were individually potted and grown until identification could be made. The soil medium ensured that the plants, which germinated, could reach a stage where they could be identified before dying down. The day/night temperatures in the greenhouse were kept between 25–30°C/15–18°C.

The seed bank was sampled two weeks after the fire (middle September, before new seeds were set), end of December (after first seasonal seed production) and end of March (after second seasonal seed production), which were considered critical periods. This was conducted one and two years after burning. The study area is characterised by these two seed production peaks under normal rainfall conditions.

Data analysis

The design was fully randomised with three replications for each treatment. All data on rate of spread and flame height were analysed using a one-way ANOVA (Winer 1974).

Within-year and between-year data were analysed separately. For seedling density, sub-sampling was employed where seedlings data were averaged across quadrats within plots and then analysed among burning treatments and sample periods. Significance between treatments was determined with Tukey's test, and the Number Cruncher Statistical System (2000) software package was used. Species richness was considered as the total number of species in the seed bank occurring within all soil samples for each burning treatment.

Results

Fire behaviour

The environmental conditions during the August 2000 and August 2001 fires were very similar. If these environmental parameters, namely above-ground phytomass production (1 453kg ha^{-1} and 1 200kg ha^{-1}), fuel-water content (18% and 21%), wind speed (2.44m s^{-1} and 2.33m s^{-1}) and relative humidity (43% and 41%), are input into the fire behaviour model of Trollope (1999) the predicted fire intensity was 1 145kJ s^{-1} m^{-1} and 766kJ s^{-1} m^{-1} for August 2000 and 2001 respectively. Therefore, the fire intensities of the two seasons ranged from a moderately hot to a cool fire (Trollope and Potgieter 1985).

The mean air temperatures during the fire measured on the control plots at ground level, 220mm and 1m aboveground were 12.2°C (±1.5), 15.4°C (±1.8) and 17.3°C (±1.9) respectively. Temperature at 10mm under the soil in case of the back and head fires varies, with a range of temperature increase of 9°C to 15°C and 9°C to 21°C, respectively. At ground level and canopy height the temperature in the back fire exceeded 100°C and 400°C respectively. In contrast the head fire had temperatures of less than 100°C at ground level, but exceeded 500°C at 1m above the ground. The reason for the higher intensity of the head fire at 1m above ground lies in the greater flame length of head fire (1.05m vs 0.52m), which ensures that this stratum above the ground still forms part of or is immediately adjacent to the zone of flaming combustion. The head fire moved 4.66m min^{-1} over the plots, compared to only 0.62m min^{-1} of the back fire, which is 7.5 times faster ($P \leq 0.01$).

Botanical composition

The species composition and mean grassland condition score of the experimental plots before the fire and four months after the fire are presented in Table 1. The experimental plots were in good condition before the fire with a grassland condition count of only 13% lower than that of a benchmark site adjacent to the burnt plots (Snyman 2000). The grassland condition score decreased with only 1.2% ($P > 0.05$) due to the fire (Table 1).

The botanical composition did not differ much between head and back fires and a mean percentage frequency of the species is presented in Table 1. As the grassland was dominated by Decreaser species before the fire, the composition after the fire was dominated by a larger percentage of Increaser IIa species. The most conspicuous decrease in frequency due to the fire were for *Themeda triandra, Cymbopogon plurinodis, Elionurus muticus* and *Digitaria eriantha*. The species increasing with fire were *D. argyrograpta* (97%), *Eragrostis chloromelas* (149%) and *Tragus koelerioides* (124%). The fact that these species split up into many smaller tufts after the fire could have resulted in an overestimation of their frequency.

Table 1: Frequency (%) of species, ecological status and veld condition score for the grassland before and four months after burning. Percentages within a row with different superscripts differ significantly ($P \leq 0.01$)

Ecological status	Species	Before fire	After fire
Decreaser	*Digitaria eriantha*	5.10	4.53
	Panicum stapfianum	0.20	0.02
	Sporobolus fimbriatus	3.16^a	2.11^b
	Themeda triandra	49.10^a	34.54^b
Decreaser total		57.56	41.20
Increaser II(a)	*Cymbopogon plurinodis*	4.14^a	0.79^b
	Digitaria argyrograpta	7.17^a	14.12^b
	Eragrostis chloromelas	10.16^a	25.29^b
	Eragrostis lehmanniana	2.92	3.15
	Eragrostis superba	1.11^a	2.10^b
	Heteropogon contortus	1.31^a	3.04^b
Increaser II(a) total		26.81	48.49
Increaser II(b)	*Eragrostis obtusa*	0.10^a	0.02^b
	Elionurus muticus	6.98^a	1.94^b
	Triraphis andropogonoides	0.02	0.02
Increaser II(b) total		7.10	1.98
Increaser II(c)	*Aristida congesta*	2.20	2.11
	Tragus koelerioides	2.33^a	5.22^b
Increaser II(c) total		4.53	7.33
Increaser II total		34.44	57.80
TOTAL		100.00	100.00
Veld condition score		796.20	786.32

Seed bank composition and size

During the soil collections at the end of December and March for the greenhouse trials, all the grasses were dormant and most had already dropped seed. The September collection took place right after the fire and therefore the grasses had scarcely begun sprouting and had no grasses seeded yet. Four days after starting the germination study in the greenhouse, the first grass seeds emerged, especially *Eragrostis* species, with small seeds, emerged first in the soil of the unburnt grassland. After seven days most grass seeds had germinated and the soil of the burnt grassland showed the highest seedling densities. After two weeks no further germination occurred. Observations were carried out for a further 10 weeks to identify all species.

The head fire increased grass seedling density more ($P \leq 0.01$) than the back fire for only December of the first season after burning (Table 2). Due to the higher intensity of the fire close to the soil surface, more seeds could possibly have been destroyed by the back fire. Generally, fire increased ($P \geq 0.01$) seedling emergence when compared to the lower number of plants m^{-2} of the unburnt plots. Most germination occurred at the end of the growing seasons, with the poorest

Table 2: Density of grass seedlings (m^{-2}) for the burnt (first [1] and second [2] season after burning) and unburnt grassland estimated in September, December and March of the 2000/01 and 2001/02 growing seasons, which were germinating in the greenhouse. UB = unburnt, H = head fire and B = back fire. Numbers within a column with different superscripts for each month differ significantly ($P \leq 0.01$). Data are means and standard error

Species	September					December					March				
	UB	H		B		UB	H		B		UB	H		B	
		1	2	1	2		1	2	1	2		1	2	1	2
Aristida congesta				2.0			4.0		2.0			12.1		24.0	
				± 0.3			±0.02		±0.1			±1.3		±2.2	
Cymbopogon plurinodes	0.5														
	±0.1														
Digitaria eriantha	0.9										1.0				
	±0.1										±0.2				
Eragrostis chloromelas	11.3	23.5	107.9	24.0	109.0	5.5	42.0	5.0	13.8	4.0	38.3	313.7	136.0	266.0	122.1
	±2.2	±4.4	±19.9	±4.2	±15.2	±2.0	±6.5	±2.2	±1.1	±0.3	±4.6	±30.1	±19.4	±29.2	±12.4
E. lehmanniana	1.9	10.8	6.1	13.5	2.0	0.5	6.0	1.1	4.0		1.0	6.1	10.1	7.9	12.0
	±0.3	±2.0	±0.8	±3.1	±0.1	±0.1	±2.1	±0.2	±0.3		±0.1	±0.3	±4.6	±0.9	±1.3
E. superba	3.3	5.9	2.0	8.0	2.0	3.5	5.0	2.3	2.0	2.0	5.0		2.2		8.0
	±1.1	±1.2	±0.9	±2.1	±0.3	±0.9	±1.4	±0.9	±0.1	±0.1	±0.2		±0.9		±1.3
Elionurus muticus	5.7	4.9	4.0	5.5	5.7	4.2	16.0	2.0	8.1	2.0	3.0	40.1	33.9	19.9	8.0
	±1.4	±0.9	±0.9	±1.4	±0.9	±0.9	±2.4	±0.9	±1.0	±0.9	±1.0	±1.0	±8.4	±3.3	±0.9
Panicum stapfianum	1.9					0.2					1.0				
	±0.9					±0.1					±0.1				
Sporobolus fimbriatus	1.9		2.1		2.0	2.0		2.0	1.0	1.0	0.6		8.0		8.0
	±0.2		±0.3		±0.1	±0.1		±0.3	±0.1	±0.1	±0.1		±1.3		±2.4
Themeda triandra	24.7	31.2	9.9	36.0	11.5	6.0	3.0	2.0		1.0	8.1		6.1		
	±5.4	±3.6	±2.1	±1.4	±1.3	±0.9	±0.2	±0.2		±0.1	±1.3		±2.1		
Tragus koelerioides		2.0		1.9								6.1		4.1	2.0
		±0.3		±0.3								±0.9		±0.4	±0.1
TOTAL	**52.1^{a}**	**78.3^{b}**	**132.0^{c}**	**90.9^{b}**	**132.2^{c}**	**21.9^{b}**	**72.0^{c}**	**14.4^{a}**	**28.9^{b}**	**10.0^{a}**	**58.0^{a}**	**378.1^{c}**	**196.3^{b}**	**315.9^{c}**	**160.1^{b}**

germination during December. The highest number of seedlings (378 plants m^{-2}) was obtained from the March soil collection in the first season with the head fire. With the exception of September, fire stimulated the grass seedling emergence more during the first season following the fire and was on average for both the head and back fires 50% more than during the second season following the burning. The grass seedling density of the unburnt plots did not differ much ($P > 0.05$) over the two growing seasons and therefore is given as an average in Table 2.

Forb seedling densities did not differ significantly ($P > 0.05$) between the head and back fires during the second season after the fire (Table 3). For the first season following the fire, seedling densities differed significantly ($P < 0.01$) between the head and back fires for only September. Interestingly, for both seasons, fire stimulated ($P \leq 0.01$) seedling emergence during the first part of the season. In contrast, over the last half of both seasons, seedling emergence was higher ($P \leq 0.01$) on unburnt than burnt grassland. Most forb seedlings, irrespective of the fire treatment, germinated during December each season. Fire stimulated higher seedling germination of the forbs in the second season after burning than during the first season, with the exception of September.

Germinable grass seeds (Table 2) of eight and nine plant species for burnt (mean for head and back fires) and unburnt grassland respectively were found in the soil cores collected. Three grass species (climax) were found in the seed bank of the unburnt grassland and not in that of burnt grassland, compared with two grass species (pioneer) found only in the burnt and not in the unburnt grassland seed bank. Species richness was therefore poorer following fire. All 11 plant species present in the seed bank were also present in the standing vegetation (Table 1). However, four species were present only in the standing vegetation (Table 1), but were not recovered in the seed bank (Table 2).

Table 3: Density of forb seedlings (m^{-2}) for burnt (first and second season after burning) and unburnt grassland germinating in the greenhouse during September, December and March. Data are means and standard error. Numbers within a row with different superscripts differ significantly ($P \leq 0.01$)

	Unburnt	Burnt	
		Head fire	Back fire
First season (2000/01)			
September	$42.2^a \pm 3.4$	$70.3^c \pm 4.0$	$58.3^b \pm 3.8$
P-value = 0.214			
December	$108.1^a \pm 6.6$	$126.5^b \pm 7.9$	$120.4^b \pm 7.2$
P-value = 0.068			
March	$77.6^b \pm 4.2$	$17.3^a \pm 1.1$	$11.8^a \pm 1.0$
P-value = 0.312			
Second season (2001/02)			
September	$34.5^a \pm 2.6$	$42.1^b \pm 3.1$	$42.6^b \pm 3.0$
P-value = 0.121			
December	$108.2^a \pm 6.8$	$165.3^b \pm 12.9$	$154.5^b \pm 6.4$
P-value = 0.086			
March	$67.2^b \pm 4.0$	$59.5^a \pm 4.8$	$55.1^a \pm 4.1$
P-value = 0.101			

Notable in Table 2 is that unburnt grassland is dominated by the species *Eragrostis chloromelas* and *Themeda triandra*. The pioneer grass species *Aristida congesta* and *Tragus koelerioides* only occurred in the burnt grassland primarily during the first season following the fire. The species *Cymbopogon plurinodes*, *Panicum stapfianum* and *Digitaria eriantha* only germinated in the unburnt plots. *Elionurus muticus* increased to a larger extent due to the fire, but *Eragrostis chloromelas* and *E. lehmanniana* showed the sharpest response due to fire. *Eragrostis lehmanniana* and *T. triandra* had higher germinating at the start of the growing season, whereas *E. chloromelas* generally showed increased emergence as the season progressed. *Themeda triandra* had a higher seedling density in the first season than in the second one after the fire. *Sporobolis fimbriatus* emerged only during the second season following the fire.

The only forb occurring in the standing vegetation was *Geigeria aspera* with a frequency of 1.12%, but it was not recovered in the seed bank. No shrubs, namely *Lycium tenue* or *Walafrida saxatilis*, emerged in the seed bank.

Discussion and Conclusions

Fire may produce the post-burn flush of seedlings in the seed bank by several direct and/or indirect means which include: (1) direct heating of the soil and seed bank, which could affect seed germination (West 1951, Trollope 1984, Keeley and Keeley 1987, Ruyle *et al*. 1988, Zacharias *et al*. 1988, Zammit and Zedler 1988, Tyler 1995), smoke-induced germination (Leck *et al.* 1989, Baskin and Baskin 1998), change in soil structure (Adams 1996) and nutrient levels (Harper 1977, Fenner 1985, Fowler 1986, Winkel *et al*. 1991, Cavers 1995, Kinloch and Friedel 2005b), and (2) temporary reduction in competition by removing aboveground vegetation (Roux 1960, McIvor and Gardener 1994, Belsky 1986, Keeley and Keeley 1987, Hulbert 1988, Moloney 1990, Swank and Oechel 1991, Milton 1995, Tyler 1995, Edwards and Crawley 1999, Maret and Wilson 2000, Jutila and Grace 2002, Kinloch and Friedel 2005a, 2005b), thereby allowing seedlings greater access to light and water (Skoglund 1992, Snyman 2004c) and reducing allelopathic influences (Keeley *et al*. 1985). The relationship between fire intensity and patterns of seedling recruitment following a wild fire is still unclear (Tyler 1995).

The overall conclusion was that back fires are more intense than head fires at ground level, whereas head fires are hotter than back fires at levels above the canopy of the grass sward. Head fires have a greater potential for developing higher temperatures than back fires at all levels, given the appropriate environmental conditions (Snyman 2003a). Although the grassland condition count (Table 1) did not decrease much as a result of fire, the short-term botanical composition varied significantly (Whisenant *et al.* 1984). The species richness of the head and back fires remained the same throughout, in spite of higher fire intensity of the back fire close to the soil. Unfortunately, only a few studies have addressed the extent to which seeds in the seed bank could recruit into the field (Sarukhan 1974, Bullock *et al*. 1994, Snyman 2004c, Kinloch and Friedel 2005a, 2005b). The soil seed bank results obtained in this study are among the few that can be linked to short-term seedling recruitment and survival in the field. Although as many as 485 and 142 seedlings m^{-2} for burnt and unburnt grassland respectively germinated in the first season after the fire, only 0.48 and 0.86 seedlings m^{-2} survived in the experimental plots in the field (Snyman 2004b). The burning of semi-arid grassland did therefore have an important impact on the survival of seedlings in the field.

The purpose of the different sampling dates in this study was to collect soil seeds at different periods to allow dormancy-breaking conditions to occur in the field and to sample transient (those seeds which germinate within a year of dispersal) and persistent (those seeds which remain viable in the soil until a second or later season of germination) components of the seed bank. Therefore an estimation of the between-year (persistent) and within-year (transient) seed bank (Thompson and Grime 1979) was made.

Caution is necessary when comparing studies of soil seed banks because of differing methods, e.g. with respect to sample size, depth, time and number of germination cycles (Snyman 2004c). The highest grass seedling density from burnt and unburnt grassland in this study of 347 and 58 seedlings m^{-2} respectively determined during March was extremely low when compared to results of seed bank studies in other countries. Mean seed densities of 4 000 seeds m^{-2} (McIvor and Gardener 1994) in the drier central and northeast Queensland, 7 639 seeds m^{-2} in central Queensland (Bahnisch *et al*. 1999), 800 seeds m^{-2} of *Eragrostis lehmanniana* in southern Arizona (Ruyle *et al*. 1988) and 2 252–4 409 seeds m^{-2} for a semi-arid grassland of the western Edwards Plateau, Texas (Kinucan and Smeins 1992), have been recorded. However, this study's results compare well with other South African seed bank studies of 172 seedlings m^{-2} in a semi-arid *Themeda triandra* grassland (Snyman 2004c), 200 seeds m^{-2} in the mesic Tall Grassveld of KwaZulu-Natal (Adams 1996) and up to 350 seeds m^{-2} from *Themeda triandra* rangeland in the semi-arid savanna (O'Connor 1997). Unfortunately, information on the influence of fire on the seed bank of grassland is lacking in the literature, because most studies concentrated on savanna regions. Perennial grasses, especially the larger-seeded species, do not, in general, form persistent seed banks even in the absence of seed predation because of poor seed survival (Williams 1983).

However, the direct and indirect influence of fire on the germination of grasses must be distinguished. To survive a fire, some grass species must achieve effective burial unless germination and establishment occur before they are normally exposed to fire (Zacharias *et al*. 1988), e.g. *Heteropogon contortus* seeds which are well adapted to and indeed promoted by, fire. According to Zacharias *et al*. (1988), *T. triandra* responded negatively to fire. This response in *T. triandra* is in direct contrast to the findings in my study and to the generally-held view that this species evolved under a consistent fire regime (Tainton 1981, O'Connor 1997). On the one hand *T. triandra* seedlings emerge most readily when the seeds lie on the soil surface (O'Connor 1997), comparing with the idea that because of the sensitivity of this species' seeds to fire, it could be postulated that reproduction in *Themeda triandra* is achieved primarily by vegetative reproduction (Zacharias *et al*. 1988). The evidence from studies in both semi-arid (Danckwerts 1984) and mesic (Everson 1985) environments supports the last suggestion.

About 40% more seedlings of *E. lehmanniana* emerged from soil surface samples taken from burnt than unburnt plots in southern Arizona (Ruyle *et al*. 1988). The same trend was observed in this study for *E. lehmanniana* (1 070%) and *E. chloromelas* (2 411%), inasmuch that *E. lehmanniana* is one of the few species which did not survive in unburnt grassland at the end of a season (Snyman 2004b). As researchers agree that most grass seeds are present in the top 50–80mm of soil (Cavers 1995, Bahnisch *et al*. 1999, Edwards and Crawley 1999), the higher soil temperatures due to fire, especially over the top soil layers, may be sufficient to break seed dormancy in some grass species in the seed bank (Auld and Bradstock 1996, Baskin and Baskin 1998). These higher soil temperatures, as well as smoke-induced germination (Leck *et al.* 1989), may be reasons for the higher seed density of the seed bank in the burnt grassland than that of the unburnt grassland in this study.

Only a few forb seedlings were found in the seed bank in spring, but as the season progressed the number of seedlings increased. The explanation for this could be that most of the forbs flowered later in the season as many seeds had been distributed by wind into the rangeland. Luckily the competition of the grasses is too strong for germination and survival of these invaders in the field (Snyman 2003c).

A short-term warning trend is that the pioneer grass species *Aristida congesta* and *Tragus koelerioides* are the only two species occurring in the seed bank (Table 2) in burnt grassland but not in unburnt grassland. During the second growing season following the fire, the impact of the fire on species richness and seed bank gradually lessened. The absence from the seed bank of several species dominating the vegetation has been reported for many grasslands (Graham and Hutchings 1988, D'Angela *et al*. 1988, Milberg 1992). Soil seed bank is an important component of vegetation dynamics affecting both ecosystem resistance and resilience (Pugnaire and Lazaro 2000).

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Edited by A-E van Wyk